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RESEARCH PAPER

The Miocene *Keramidomys* (Rodentia, Eomyidae) from the Sandelzhausen locality (Germany)

Pierre Mein

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Abstract In this note the taxonomic position of the tiny eomyid genus *Keramidomys* (Hartenberger, 1967) from the Early/Middle Miocene boundary locality of Sandelzhausen in the Bavarian Upper Freshwater Molasse is reexamined. As the chronological dating of the Sandelzhausen fossil site has been modified in the past from formerly the Neogene mammal unit MN6 to now MN5 and thanks to new abundant material this rodent is compared with other European forms. It is shown that the Sandelzhausen eomyid must be called *K. thaleri* Hugueney & Mein, 1968 on the basis of several morphological dental differences from *K. carpathicus* Schaub & Zapfe, 1953. This rodent seems to be an immigrant from East Asia into Europe. Even if *K. thaleri* is known in many European localities, all correlated to MN5, it is always a rare element of European rodent faunas. Differentiation from *K. carpathicus* is not easy and requires a sufficiently large sample.

Keywords Rodents · *Keramidomys* · Miocene · MN5 · Sandelzhausen · Bavaria

Kurzfassung Diese Untersuchung widmet sich der Überprüfung der taxonomischen Stellung der sehr kleinwüchsigen Eomyiden-Gattung *Keramidomys* (Hartenberger, 1967) aus der bayerischen Oberen Süßwassermolasse der Lokalität Sandelzhausen. Die Alterseinstufung der Fauna von Sandelzhausen wurde in der Vergangenheit mehrmals korrigiert und wird nun der Säugetier-Stufe MN5–im Grenzbereich von Unter-zu Mittelmiozän–zugeordnet. Die vorliegende Arbeit stellt ein neues, reichhaltiges Material von *Keramidomys* aus Sandelzhausen vor, das umfangreiche Vergleiche mit anderen europäischen Formen erlaubt. Der Eomyide aus Sandelzhausen kann auf der Basis zahlreicher morphologischer Unterschiede zu *K. carpathicus* Schaub & Zapfe, 1953 als *K. thaleri* Hugueney & Mein, 1968 bestimmt werden. *Keramidomys* scheint aus Ostasien nach Europa eingewandert zu sein und ist stets ein seltenes Faunenelement in den europäischen Nagetierfaunen, auch wenn es aus vielen europäischen Lokalitäten der Säugetier-Zone MN5 bekannt ist. Die Unterscheidung von *K. thaleri* und *K. carpathicus* ist nicht einfach und bedarf einer ausreichend großen Materialmenge.

Schlüsselwörter Nagetiere · *Keramidomys* · Miozän · MN5 · Sandelzhausen · Bayern

P. Mein (✉)
Département des Sciences de la Terre,
Université Claude Bernard I,
27-43 boulevard du,
69621 Villeurbanne Cedex, France
e-mail: pierre.mein@univ-lyon1.fr

Introduction

The vertebrate fossil site Sandelzhausen is located in the Bavarian North Alpine Foreland Basin (Southern Germany), near the town of Mainburg, about 70 km north of Munich. The limnofluvial deposits of Sandelzhausen belong to the Upper Freshwater Molasse. Based on mammal biostratigraphy the Sandelzhausen fauna was referred to the European Mammal Neogene Unit MN5 by Heissig (1997). Based on recent bio-, litho- and magnetostratigraphic analyses the stratigraphic position of the locality Sandelzhausen is situated at or very close to the Early/Middle Miocene boundary (Karpatian/Badenian boundary) (Moser et al. 2009, this volume).

Fahlbusch (1975) was the first to study the specimens of this family from Sandelzhausen but at that time he had only 25 teeth at his disposal; since then 300 additional teeth have been collected so that it is possible now to have a better view of variation in the group.

The Eomyidae is an extinct family of myomorphous rodents which lived throughout the Holarctic region during most of the Cenozoic Era; they appeared in Europe during the Lower Oligocene and were very numerous and diversified. Often they were the dominant small mammals in the Upper Oligocene and the Lower Miocene.

Two major syntheses of this group have been published: Fahlbusch (1979) gave a complete schema and Engesser (1999) wrote about the European forms. According to these papers, the Eomyids declined during MN4 at the end of which the last genus *Ligerimys* Stehlin & Schaub, 1951 vanished. At about the same time, two new genera appeared in Europe: *Keramidomys* (Hartenberger, 1967) and *Eomyops* (Engesser, 1979), the latter genus remaining very rare during MN5 and MN6. To date, only two localities have yielded the genus *Keramidomys* in association with the genus *Ligerimys*: from France Vieux Collonges and from Poland Belchatow B. From Gashunyindege (China) Qiu & Wang (1999) mentioned *Keramidomys* and *Leptodontomys* Shotwell, 1956 (=*Eomyops*) at the beginning of MN4. Some years ago it was thought that *Keramidomys* was a local successor to *Pseudotheridomys* Schlosser, 1926; this hypothesis, which would imply a size reduction and a Lazarus effect, is no longer supported today. More probably it seems that both genera originated in East Asia. Sandelzhausen has yielded only one eomyid genus: *Keramidomys*. Although these two genera were never common they survived until the beginning of the Quaternary Epoch. Fahlbusch & Bolliger (1996) gave a list of the European localities where *Keramidomys* and *Leptodontomys* are present; in this paper, Table 1 lists the known localities for *Keramidomys* during MN5 and MN6. Later different species may coexist but they remain rare and occur in only a few localities.

Table 1 MN5 and MN6 localities with *Keramidomys*

MN5 localities with *Keramidomys*
Spain
Lumiar 7 (Daams, personal communication)
Vargas 7 g (Daams, personal communication)
France
Lo Fournas 2 (Aguilar et al. 1986)
Vieux Collonges (Hugueney and Mein 1968)
Switzerland
Chatzloch (Kälin 1997)
Chlaustobel (Bolliger 1992)
Güntisberg (Bolliger 1992)
Hombrechtikon-Hotwiel (Bolliger 1992)
Hombrechtikon-Sperstr. (Bolliger 1992)
Hombrechtikon-Tobel (Engesser 1990)
Hüllistein (Bolliger 1992)
Martin brünneli (Kälin 1997)
Stäfa-Burgistobel A (Bolliger 1992)
Stäfa-Schliffitobel B (Bolliger 1992)
Vermes 1 (Engesser 1990)
Vermes 2 (Kälin 1997)
Werthenstein-Grabenhüsli (Engesser 1990)
Bohemia
Franzenbad (Fejfar 1974)
Strakonice (Fejfar 1974)
Germany
Adelschlag (Fahlbusch 1975)
Edelbeuren-Maurerkopf (Sach 1999)
Eitensheim (Fahlbusch 1975)
Engelwies 1 (Ziegler 1995)
Gisseltshausen 1b (Heissig 1989)
Gundlkofen (Fahlbusch 1975)
Hambach C (Mörs et al. 2000)
Langenmoosen (Fahlbusch 1975)
Massendorf (Schötz 1979)
Niederreichbach (Schötz1979)
Oggenhof (Fahlbusch 1975)
Pöttmes (Fahlbusch 1975)
Puttenhausen (Fahlbusch and Wu 1981)
Rosshaupten (Fahlbusch 1975)
Sandelzhausen (Fahlbusch 1975)
Schönenberg (Fahlbusch 1975)
Undorf (Fahlbusch 1975)
Unterneul 1a (Heissig 1989)
Obergänserndorf (Daxner-Höck 1998)
Teiritzberg (Daxner-Höck 1998)
Poland
Belchatow (Kowalski and Rzebik-Kowalski 2002)
Turkish Republic
Candir (De Bruijn et al. 2003)

Materials and methods

The material presented here is housed at the Bayerische Staatssammlung für Paläontologie und Geologie Munich (BSPG) under the collection number BSPG 1959 II xxxxx; in the following, only the last part of the inventory number is given. The entire material is listed in Tables 2, 3, 4, 5 and 6. For the description, the dental terminology proposed by Engesser (1999) is used. Following abbreviations indicate the different tooth positions: upper deciduous molar (D), premolars (P), and molars (M) and lower deciduous molar (d), premolars (p) and molars (m).

Table 1 continued

MN6 localities with *Keramidomys*
France
Sansan (Engesser 1979)
Switzerland
Chatzloch (Kälin 1997)
Chrüzbuel-Ruehalden (Bolliger 1992)
Gerstel (Bolliger 1992)
Schauenberg (Bolliger 1992)
Germany
Gallenbach 3a2b (Heissig 1989)
Unterzolling 1a (Heissig 1989)
Slovakia
Neudorf Spalte (Fejfar 1974; Daxner-Höck 1998)
Poland
Opole 2 (Kowalski 1967)
Turkish Republic
Pismanköy (Unay and de Bruijn 1984)
Central Mongolia
Ulaan Tolgoi (Höck et al. 1999)

Research history of the taxon *Keramidomys*

The genus *Keramidomys* was erected by Hartenberger (1967) for the Lower Vallesian species from Can Llobateres (Spain): *Keramidomys pertesunatoi* Hartenberger, (1967). Soon afterwards Hugueney & Mein (1968) included in this genus a new species from the Lower Middle Miocene of Vieux Collonges (France): *Keramidomys thaleri*, characterised by a long syncline I in the M1 and M2.

The original diagnosis for *K. thaleri* is as follows (translated from French from Hugueney & Mein, 1968):

"Very small eomyid with a relatively high crown and a plane occlusal surface. m1 and m2 have four roots; P4 and m3 are smaller and less complicated than the other teeth that differentiate them from *Pseudotheridomys* teeth; this species differs from *K. pertesunatoi* Hartenberger (1967) and from *Keramidomys carpathicus* Schaub & Zapfe (1953) because of the unreduced first buccal syncline in upper molars and in the always well-preserved mesoloph and mesolophid".

It was Hugueney & Mein (1968) who referred *Pseudotheridomys carpathicus* Schaub & Zapfe (1953), described from Neudorf Spalte (Slovak Republic), to *Keramidomys*. This last species was reexamined and figured in Fejfar (1974), who described its great morphological variability and showed some teeth with a long syncline. Fahlbusch (1975) studying new material from the Upper Freshwater Molasse of Bavaria concluded that the sample of *K. thaleri* is too small to provide a good idea of the variability and does not present really discriminant characteristics. So, he preserved only the name *K. carpathicus* for the small eomyids from MN5 and MN6. Many scholars followed this opinion, including Schötz (1979), Bolliger (1992), Ziegler (1995) and Mörs et al. (2000).

From some Swiss Molasse localities Engesser (1990) expressed an opposite position and distinguished *K. thaleri* in MN5 from *K. carpathicus* in MN6. He observed that the M3 of *K. thaleri*, which was unknown from Vieux Collonges, shows a long mesoloph whereas this crest is reduced or even absent in *K. carpathicus*; the mesolophid on m3 is also more reduced in the latter species.

Later, Heissig (1997) showed in a biostratigraphical framework of the Bavarian Upper Freshwater Molasse that

Table 2 Measurements (mm) of D4, P4, M3 of *Keramidomys thaleri* from Sandelzhausen, including mean and standard deviation

Inventory no.	Length	Width	Inventory no.	Length	Width
D4			P4		
10037 sin.	0.76	0.69	5387 sin.	0.67	0.75
10038 sin.	0.74	0.77	10015 sin.	0.71	0.77
10039 sin.	0.63	0.63	10016 sin.	0.66	0.72
10040 sin.	0.76	0.71	10017 sin.	0.70	0.82
10041 sin.	0.65	–	5398 sin.	0.60	0.73
10042 sin.	0.66	0.69	10018 dext.	0.69	0.79
10043 sin.	0.66	0.72	10019 dext.	0.71	0.83
10044 sin.	0.72	0.73	10020 sin.	0.63	0.74
10045 dext.	0.72	0.75	10021 sin.	0.71	0.77
10046 dext.	0.71	0.73	10022 sin.	0.63	0.70
10047 dext.	0.67	0.71	10023 sin.	0.64	0.73
10048 dext.	0.78	0.78	10024 sin.	0.67	0.76
10049 dext.	0.75	0.75	10025 sin.	0.66	0.75
10050 dext.	0.76	0.75	10026 sin.	0.69	0.80
10051 dext.	0.78	0.78	10027 sin.	0.65	0.71
10052 dext.	0.74	0.73	10028 sin.	0.66	0.76
10053 dext.	0.74	0.74	5522 dext.	0.66	0.77
10054 dext.	0.68	0.67	10029 sin.	0.67	0.73
10055 dext.	0.77	0.77	5399 sin.	0.71	0.80
10056 dext.	0.71	0.75	10030 dext.	0.66	0.76
5386 dext.	0.71	0.75	10031 dext.	0.66	0.78
5401 dext.	0.85	0.78	10032 dext.	0.65	0.79
Mean	0.725	0.7324	10033 dext.	0.65	0.74
SD	0.0523	0.0390	10034 dext.	0.71	0.84
			10035 dext.	0.67	0.77
M3			10036 dext.	0.68	0.76
413 sin.	0.54	0.68	484 sin. c. 6j	0.75	0.82
414 sin.	0.52	0.69	485 dext. fig. 6k	0.67	0.75
415 dext.	0.59	0.66	10303 dext.	0.65	0.75
416 dext.	0.50	0.60	Mean	0.6714	0.7652
Mean	0.5375	0.6575	SD	0.0313	0.0354
SD	0.0386	0.0403			

The full inventory number of each specimen is BSPG 1959 II plus the given number. Cited figures are in Fahlbusch 1975

Table 3 Measurements (mm) of M1-2 of *Keramidomys thaleri* from Sandelzhausen, including mean and standard deviation

Inventory no.	Length	Width	Inventory no.	Length	Width
M1-2 (M1)			M1-2 (M2)		
10333 sin.	0.76	0.86	10348 sin.	0.65	0.85
10334 sin.	0.73	0.86	10349 sin.	0.73	–
10335 sin.	0.72	0.79	10350 sin.	0.66	0.77
10337 sin.	0.78	0.90	10351 sin.	0.72	0.81
10338 sin.	0.80	0.85	10352 sin.	0.69	0.85
10339 sin.	0.78	0.84	10353 sin.	0.65	0.80
10340 sin.	0.72	0.76	10354 sin.	0.64	0.76
10341 sin.	0.74	0.76	10355 sin.	0.66	0.75
10342 sin.	0.77	0.82	5404 sin.	0.62	0.74
10343 sin.	0.76	0.87	5405 sin.	0.65	0.85
10344 sin.	0.74	0.87	5406 sin.	0.69	0.85
10345 sin.	0.73	0.78	10356 sin.	0.65	0.79
10346 sin.	0.75	0.84	10357 sin.	0.67	0.80
5523 sin.	0.77	0.88	10358 sin.	–	0.81
10347 sin.	0.80	0.84	10359 sin.	0.62	–
10360 dext.	0.71	0.83	5524 sin.	0.80	–
10361 dext.	0.74	0.78	10336 sin.	0.63	0.71
10362 dext.	0.76	0.89	10377 dext.	0.65	0.80
10363 dext.	0.72	0.86	10378 dext.	0.68	0.80
10364 dext.	0.76	0.84	10379 dext.	0.67	0.80
5383 dext.	0.77	0.81	10380 dext.	0.67	0.82
5400 dext.	0.70	0.78	10381 dext.	0.72	0.87
5402 dext.	0.78	0.85	10382 dext.	0.69	0.85
5403 dext.	0.76	0.87	10383 dext.	0.69	0.86
10365 dext.	0.80	0.90	10385 dext.	0.68	0.89
10366 dext.	0.76	0.85	10386 dext.	0.69	0.86
10367 dext.	0.76	0.85	10387 dext.	0.65	0.80
10368 dext.	0.80	0.88	5407 dext.	0.66	0.80
10369 dext.	0.76	0.84	10387 dext.	0.65	0.80
10370 dext.	0.77	0.89	10388 dext.	0.64	0.80
10371 dext.	0.76	0.85	10389 dext.	0.66	0.81
10372 dext.	0.77	0.89	10390 dext.	0.62	0.77
10373 dext.	0.74	0.84	10391 dext.	0.59	0.77
10374 dext.	0.74	0.85	10392 dext.	0.60	0.83
10375 dext.	0.79	0.86	5525 dext.	0.62	–
10376 dext.	0.77	0.87	486 sin. fig. 6n	0.60	0.78
489 dext. fig. 6m	0.74	0.85	487 sin. fig. 6o	0.69	0.80
490 dext. fig. 6l	0.79	0.84	488 sin. fig. 6p	0.67	0.80
10384 dext.	0.75	0.86	Mean	0.6627	0.8074
Mean	0.7577	0.8449	SD	0.0405	0.0395
SD	0.0257	0.0366			

The full inventory number of each specimen is BSPG 1959 II plus the given number. Cited figures are in Fahlbusch 1975

Table 4 Measurements (mm) of m1-2 of *Keramidomys thaleri* from Sandelzhausen, including mean and standard deviation

Inventory no.	Length	Width	Inventory no.	Length	Width
m1-2			m1-2		
5395 sin.	0.75	0.80	482 dext.	0.73	0.76
10282 sin.	0.76	0.77	483 dext. fig. 6f	0.78	0.76
10283 sin.	0.76	0.76	5384 dext.	0.82	0.79
10284 sin.	0.76	0.73	10309 dext.	0.79	0.78
10285 sin.	0.83	0.82	10310 dext.	0.78	0.81
10286 sin.	0.79	0.78	10311 dext.	0.80	0.77
10287 sin.	0.83	0.80	10312 dext.	0.71	0.69
10288 sin.	0.73	0.74	5385 dext.	0.72	0.75
10289 sin.	0.79	0.80	10313 dext.	0.76	0.72
10290 sin.	0.76	0.73	10314 dext.	0.76	0.77
10291 sin.	0.66	0.78	10315 dext.	0.76	0.78
10292 sin.	0.69	0.74	10316 dext.	0.81	0.82
10293 sin.	0.75	0.73	10317 dext.	0.74	0.77
10294 sin.	0.76	0.77	10318 dext.	0.76	0.71
10295 sin.	0.72	0.76	10319 dext.	0.77	0.76
10296 sin.	0.72	0.76	10320 dext.	0.71	0.76
10297 sin.	0.70	0.72	10321 dext.	0.77	0.80
10298 sin.	0.79	0.76	10322 dext.	0.76	0.74
10299 sin.	0.78	0.75	10323 dext.	0.79	0.71
10300 sin.	0.80	0.81	10324 dext.	0.82	0.81
10301 sin.	0.69	0.77	10325 dext.	0.81	0.80
10302 sin.	0.66	0.68	10326 dext.	0.71	0.71
10304 sin.	0.72	0.77	10327 dext.	0.77	0.73
10305 sin.	0.75	0.79	5393 dext.	0.76	0.74
10306 sin.	0.78	0.76	5438 dext.	0.79	0.74
10307 sin.	0.71	0.78	10328 dext.	0.67	0.70
5526 sin.	0.72	0.75	10329 dext.	0.76	0.80
72 dext. fig. 6h	0.76	0.78	10330 dext.	0.80	0.85
473 sin.	0.75	0.78	10331 dext.	0.74	0.70
474 sin.	0.81	0.84	10332 dext.	0.79	0.80
475 sin.	0.80	0.78	5394 dext.	–	0.78
476 sin.	0.78	0.79	5518 dext.	0.62	0.67
477 sin. fig. 6e	0.77	0.82	417 dext.	0.76	0.77
478 dext. fig. 6g	0.77	0.75	5521 dext.	0.68	0.66
479 dext.	0.80	0.80	Mean	0.7570	0.7638
480 dext.	0.85	0.81	SD	0.0447	0.0392
481 dext. fig. 6j	0.74	0.76			

The full inventory number of each specimen is BSPG 1959 II plus the given number. Cited figures are in Fahlbusch 1975

the Sandelzhausen fauna is older than was expected. In his opinion this fauna belongs to the lithostratigraphic unit OSM-C within MN5 and not to MN6. So, the *Keramidomys* found in Sandelzhausen must be chronologically linked to *K. thaleri* from Vieux Collonges. Furthermore many localities studied in Fahlbusch (1975) and mentioned in Fahlbusch & Bolliger (1996) in spite of the poor material probably contained the same species. Daxner-Höck (1998) worked on an important collection from two localities in Austria: Teiritzberg and

Table 5 Measurements (mm) of d4, p4, m3 of *Keramidomys thaleri* from Sandelzhausen, including mean and standard deviation

Inventory no.	Length	Width	Inventory no.	Length	Width
d4			m3		
631 sin.	0.81	0.60	10393 sin.	0.60	0.62
632 sin.	0.78	0.60	10394 sin.	0.69	0.63
633 sin.	0.82	0.60	10395 sin.	0.71	0.72
634 sin.	0.77	0.60	5396 sin.	0.64	0.63
635 sin.	0.83	0.59	10396 sin.	0.68	0.60
636 sin.	0.78	0.58	1039 sin.	0.71	0.66
637 sin.	0.81	0.58	10398 sin.	0.65	0.67
638 dext.	0.77	0.52	10399 sin.	0.60	0.64
Mean	0.7962	0.5837	10400 sin.	0.64	0.63
SD	0.02	0.03	5519 sin.	0.67	0.65
			10401 dext.	0.64	0.64
p4			10402 dext.	0.71	0.64
533 sin.	0.72	0.66	10403 dext.	0.65	0.74
534 sin.	0.73	0.66	10404 dext.	0.67	0.62
535 sin.	0.76	0.69	10405 dext.	0.72	0.63
536 sin.	0.71	0.64	10406 dext.	0.68	0.68
537 sin.	0.74	0.67	10407 dext.	0.68	0.66
538 sin.	0.71	0.65	10408 dext.	0.65	0.66
539 sin.	0.73	0.63	10409 dext.	0.60	0.64
540 sin.	0.74	0.64	5397 dext.	0.69	0.70
541 sin.	0.76	0.72	5520 dext.	0.69	0.70
542 dext.	0.74	0.66	10410 dext.	0.62	0.64
543 dext.	0.67	0.65	10411 dext.	0.68	0.71
544 dext.	0.72	0.65	10412 dext.	0.61	0.63
545 dext.	0.71	0.7	Mean	0.6617	0.6558
546 dext.	0.71	0.66	SD	0.0365	0.0356
547 dext.	0.67	0.6			
548 dext.	0.77	0.67			
549 dext.	0.67	0.63			
550 dext.	0.67	0.67			
551 dext.	0.75	0.68			
5388 dext.	0.77	0.72			
5392 dext.	0.76	0.65			
467 sin.	0.72	0.69			
468 dext.	0.78	0.66			
469 dext. (fig. 6b)	0.75	0.67			
470 dext. (fig. 6a)	0.77	0.74			
471 dext. (fig. 6c)	0.76	0.63			
472 dext. (fig. 6d)	0.73	0.69			
Mean	0.7304	0.6659			
SD	0.0330	0.0312			

The full inventory number of each specimen is BSPG 1959 II plus the given number. Cited figures are in Fahlbusch 1975

Obergänserndorf, both belonging to MN5. The material was compared in detail with the MN6 collection from Neudorf Spalte (Slovak Republic). In conclusion, she recognised the validity of two different species and defined explicit new differential characters. For *K. thaleri*, the mesoloph length is greater and the mesolophid is more developed in the d4 and on the p4. Moreover in the M2, the longitudinal crest is complete in 10% of the sample, though this crest is always interrupted in *K. carpathicus*. Therefore it is necessary to have a sufficient sample to provide a positive determination. However, Obergänserndorf is an unusual site where the genus *Keramidomys* represents 32% of the rodent fauna; in all the other known Early/Middle Miocene localities this proportion is less than 1%.

Finally, Fahlbusch (2003) published a revised list of the Sandelzhausen fauna with *K. thaleri* being the only eomyid.

Description of *K. thaleri* from Sandelzhausen

The Sandelzhausen site yielded a great number of teeth of this species but among the huge number of rodent teeth it is not especially well represented. Measurements of Sandelzhausen teeth are given in Tables 2, 3, 4, and 5, and for comparisons measurements of Vieux Collonges (France) teeth are listed in Table 6.

Upper dentition

The tooth size of each category is nearly the same. The width is only slightly larger than the length; all teeth have three roots. Determining the intermediate teeth (M1 and M2) is not easy. Numerous maxillae were found only in Neudorf Spalte. Fejfar (1974), Engesser (1990) and Daxner-Höck (1998) mentioned that M1s are larger than M2s with a rounded posterior edge, whereas M2 are smaller with a straight posterior margin. The length/width dispersion diagrams largely overlap; in stratigraphically younger sites the size difference becomes more important (Fig. 1).

D4

Twenty-two teeth were collected, of which two are worn or damaged.

These teeth show a buccal border that is longer than the lingual one, which can be reduced imparting a trapezoidal outline to the tooth. The anteroloph is well developed in the buccal part where it joins the protoloph in 13 teeth out of 22. In two teeth this crest is short and ends before it connects with the protoloph. In five teeth this crest is completely fused to the protoloph. In 20 teeth the longitudinal crest is completely broken behind the protocone and in only two teeth (nos. 10048 and 10055) does it show

Table 6 Measurements (mm) of teeth of *Keramidomys thaleri* from Vieux Collonges (France) including mean and standard deviation

Inventory no.	Length	Width	Inventory no.	Length	Width
D4			D4		
No Nr. sin.	0.16	0.71	65334 sin.	0.78	0.58
No Nr. sin.	0.77	0.78	65335 sin.	0.67	–
Mean	0.465	0.745	Mean	0.725	
SD	0.4313	0.0495	SD	0.0778	
P4			p4		
65325 dext. (fig. 18)	0.70	0.80	65336 sin.	0.72	0.68
No Nr. sin. (fig. 8)	0.70	0.82	65337 dext.	0.76	0.67
No Nr.	0.69	0.79	65338 dext. (fig. 13)	0.75	0.63
No Nr.	0.71	0.79	65339 dext.	0.70	0.63
Mean	0.70	0.8	No Nr. sin.	0.79	0.70
SD	0.01	0.01	No Nr.	0.72	0.74
			No Nr. sin.	0.77	0.75
M1			Mean	0.7444	0.6857
65326 dext. (fig. 19)	0.80	0.91	SD	0.0318	0.0479
65327 dext.	0.75	0.87			
6328 dext. (fig. 20)	0.76	0.80	m1		
65329 dext.	0.76	0.87	No Nr. dext.	0.73	0.75
65332 sin.	0.77	0.84	No Nr. dext.	0.76	0.76
No Nr. sin.	0.76	0.79	No Nr. dext.	0.76	0.78
No Nr. dext.	0.76	0.86	No Nr. (fig. 8d)	0.75	0.74
No Nr. dext.	0.80	0.91	Mean	0.75	0.7575
Mean	0.7703	0.8564	SD	0.0171	0.0171
SD	0.0197	0.0445			
			m2		
M2			65340 sin. (fig. 15)	0.69	0.78
65330 dext.	0.73	0.83	65341 sin.	0.72	0.76
65331 sin.	0.71	0.83	No Nr. sin.	0.74	0.77
6333 sin. (fig. 21)	0.61	0.78	No Nr. dext.	0.74	0.76
No Nr. sin.	0.74	0.83	Mean	0.7225	0.7675
No Nr. sin.	0.80	0.92	SD	0.0236	0.0096
No Nr. dext.	0.75	0.85			
No Nr. dext.	0.75	0.92	m3		
Mean	0.7271	0.8514	65343 sin. (fig. 16)	0.62	0.63
SD	0.0585	0.0515	65342 dext. (fig. 17)	0.61	0.58
			No Nr. sin	0.66	0.64
			Mean	0.63	0.6167
			SD	0.0265	0.0321

All specimens are from the collection of the University Claude Bernard–Lyon 1 (Faculté des Sciences Lyon, FSL). For the specimens which are inventoried the complete inventory number is: FSL xxxxx. Cited figures are in Hugueney & Mein 1968

a connection between the longitudinal crest and the protoloph; so generally a deep valley crosses the tooth from the sinus to the buccal syncline II. In 15 out of 22 teeth (68%) the mesoloph is long, in 6 (27%) it is medium, and in 1 (5%) it is short. In one tooth (no. 5401) the mesoloph extends forwards and ends buccally at the paracone.

P4

In the genus *Keramidomys* the P4 has no anteroloph whereas in the oldest European species *K. thaleri* a small anteroloph followed in a shallow syncline I can be present in unworn teeth. In the type locality of Vieux Collonges

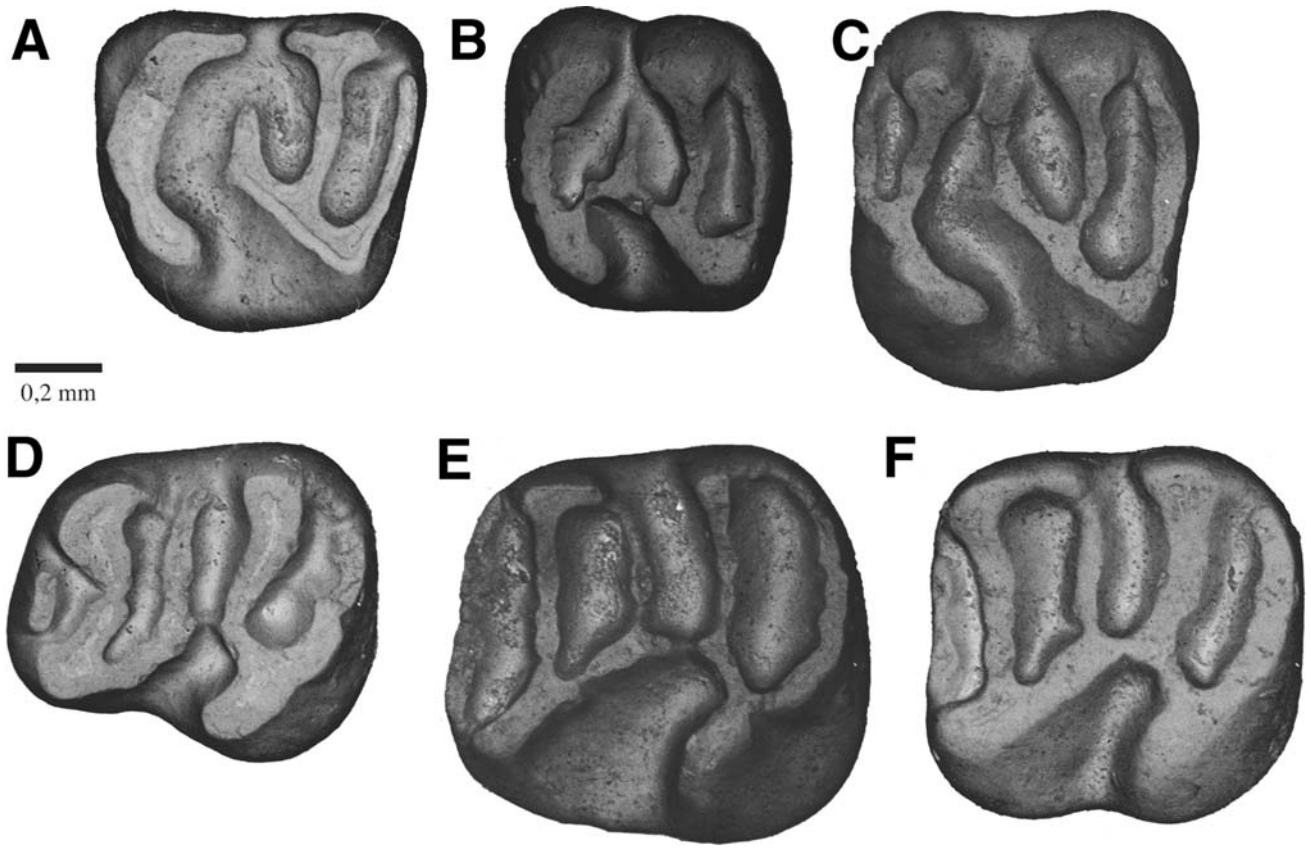

Fig. 1 Teeth of *Keramidomys thaleri* from Sandelzhausen (MN5), all in occlusal view: **a** D4 sin. (BSPG 1959 II 5386), **b** P4 sin. (BSPG 1959 II 5387), **c** M1 dext. (BSPG 1959 II 5383), **d** p4 dext. (BSPG 1959 II 5388), **e** m1 dext. (BSPG 1959 II 5384) and **f** m2 dext. (BSPG 1959 II 5385)

one P4 out of four shows this typical structure. From Sandelzhausen 4 teeth out of 29 [no. 485 (illustrated in Fahlbusch 1975: fig. 8k), nos. 10018, 10026, 10303] display the same structure. This character is not mentioned in Daxner-Höck (1998) but the figured P4 (Daxner-Höck 1998: fig. 2) has a small anteroloph in its buccal part. This character does not occur in Neudorf Spalte and Sansan. In the Sandelzhausen teeth, the longitudinal crest is complete in 16 teeth out of 28 specimens; in three teeth this crest becomes thinner and lower backwards and ends at the base of the anteroloph; in ten teeth the same crest is interrupted and a deep valley runs from the sinus to the buccal syncline II. One tooth (no. 10303) with a broken longitudinal crest exhibits a second one in the buccal part between the protoloph and metaloph. In Vieux Collonges (France), two teeth out of four have a complete longitudinal crest: one [see Fahlbusch (1975): fig. 8e] ends at the base of the protoloph and one has a broken longitudinal crest. In Sandelzhausen the mesoloph is of medium size in 20 teeth, long in 4 teeth, and short in 5 teeth. In Obergänserndorf, the majority of P4s have the mesoloph of medium length but in Neudorf Spalte this crest is short. I noted a tooth (no. 10034) with a peculiar morphology: its longitudinal crest is complete and well connected to the protoloph but the protocone is separated from the protoloph and there is a medial valley following the sinus.

M1–M2

Seventy-six M1–2 are represented and tentatively separated into 36 M1 and 40 M2.

The anteroloph is well developed lingually connected to the protoloph. In four specimens the protoloph ends at the base of the protocone. In 20 teeth the anteroloph is buccally connected to the paracone. The first buccal syncline is always clearly visible. The longitudinal crest is broken in 62 teeth. In four teeth there is a connection of this crest with the base of the protoloph (Fahlbusch 1975: fig. 6h). In nine other teeth this longitudinal crest is high and complete (Fahlbusch 1975: fig. 6o). These 13 teeth are all supposed to be M2 in spite of the large size of three of them (nos. 10343–10345). The mesoloph is long in 68 teeth, medium sized in 7, and short in 1. A thin ectoloph can be observed in 13 teeth (Fahlbusch 1975: fig. 6). When the ectoloph is incomplete we can often see a buccal connection between the mesoloph and paracone and also between the metacone and posteroloph. In a small M2 (no. 10336) the longitudinal crest is almost absent and the medium part

of the mesoloph is isolated but a new and weak lingual connection appears between protocone and hypocone (endoloph); this peculiar morphology can be seen in 25% of the M2s from Obergänserndorf (Daxner-Höck 1998: 374) but in only one specimen from Sandelzhausen. By comparison, in Vieux Collonges 15 M1–2s have been collected; only one M2 has a complete longitudinal crest, the mesoloph is long in 13 teeth and medium sized in 2. The well-developed first buccal syncline the length of the mesoloph and the presence of a complete longitudinal crest in 10% of M2 indicates that these specimens should be attributed to *K. thaleri*.

M3

Only four M3 have been found at Sandelzhausen. These teeth are smaller and more triangular than the M1–2 with a narrow lingual border. These teeth show five lophs; the anteroloph is followed in a long syncline I. In tooth no. 415 the protoloph ends before the protocone so the buccal synclines I and II are communicating.

Lower dentition

The d4 and the p4 have two roots whereas the m1 and m2 have four roots: two anterior and two posterior, while the m3 shows three roots: two anterior and one posterior; this special radiculation seems to be constant among all the species of *Keramidomys*.

d4

Eight specimens have been found in Sandelzhausen.

It is an elongated tooth narrow in the front with four lophids. The anteroconid is short and isolated in four teeth out of eight. It can form an arcuate crest connected both to the protoconid and the metaconid (one case out of eight) or be connected only to the metaconid (one case out of eight) or the protoconid (one case out of eight). In one tooth (no. 634) the anteroconid is split into two parts, the first connected to the protoconid and the other to the metaconid. The longitudinal crest is complete from protolophid to hypolophid (one case out of eight) but thinner behind the protoconid (three cases out of eight) or disappears between the protoconid and mesoconid. The long mesolophid reaches the lingual edge; it is connected with the metaconid (seven cases out of eight). The sinusid is oriented backwards.

Two d4s have been collected at Vieux Collonges; one has an interrupted longitudinal crest; the other is an aberrant tooth without anteroconid. Both have a long mesolophid.

p4

Twenty-seven specimens have been collected from Sandelzhausen.

The permanent premolar is stouter than the deciduous tooth. The anterolophid is developed as a fifth lophid in 25 teeth; in the two other teeth it is reduced to a single cuspid. Usually the anterolophid is connected with the protoconid (24 teeth); it can also connect to the metaconid (five teeth). The mesolophid is long in only one tooth (no. 534); usually it does not reach the lingual edge; it is often lingually connected with the metaconid (in 16 teeth) and is seldom connected with the enteroconid, forming a small entolophid (in two teeth); its buccal end can be swollen into a small mesoconid (three teeth). The longitudinal crest is complete in 25 teeth out of 27; in one tooth (no. 542) this crest is cut between mesolophid and hypolophid, and in the tooth no. 544 there is no longitudinal crest.

In comparison, seven p4s are known from Vieux Collonges, all of which show five lophids. The anterolophid is connected only with the protoconid. The long mesolophid is often thinner than the other lophids. In one tooth this crest is interrupted in the middle. At the buccal end of the mesolophid two teeth exhibit one mesoconid (Hugueney & Mein 1968: fig. 13). The longitudinal crest is complete. In one tooth (FSL 65349) the hypolophid does not reach the longitudinal crest buccally.

In *K. carpathicus* the anterolophids and the mesolophids are notably more reduced.

m1–m2

The Sandelzhausen locality yielded 71 isolated m1 or m2 teeth, but it is nearly impossible to separate all the specimens into m1 or m2. It is accepted in general that the larger ones belong to the m1s and the smaller ones to the m2s. If the width-to-length ratio is less than 1, the tooth is probably an m1; if the same ratio is more than 1.1, the tooth is probably an m2. Fejfar (1974: fig. 17) showed for *K. carpathicus* that the anterior roots of m2 are more spindly than the posterior ones, but this criterion is not observable in *K. thaleri*. An attempt at discrimination by using the interstitial facets of mesial and distal edges was not conclusive. The anterolophid is long in 64 teeth out of 71, medium sized in 5, and broken in the middle in 2. Lingually the mesolophid of ten teeth connects the metaconid (Fahlbusch 1975: fig. 6f–j). In one tooth (no. 479) a small entolophid can be seen. The longitudinal crest is always complete. The Vieux Collonges site yielded eight teeth. The long mesolophid connects lingually to the metaconid in four teeth.

m3

Twenty-four teeth have been collected, among which two are heavily worn but they surely had five lophids.

The anterolophid is well developed, usually connected with the protoconid, sometimes with the metaconid. Three teeth show a connection of this crest to the protolophid in the middle of the tooth; this morphology has been illustrated in Engesser (1990: fig. 107c).

The protolophid is long. From the metaconid a lingual crest often joins the different lophids, forming an entolophid. The buccal syncline I is not reduced. The mesolophid may be long (in 14 teeth out of 24), medium sized in four teeth, cut into two parts in three teeth. This crest is absent in one tooth (no. 408) so this specimen shows only four lophids whereas the other have five. In two teeth the mesolophid is connected to the hypolophid in a longitudinal connection. Only three m3s have been found at Vieux Collonges, of which two are figured in Hugueney & Mein (1968); the additional one has a long anteroconid lingually connected to the metaconid. The synclinid 1 is well developed; the mesolophid interrupted in the middle ends lingually in a stylid.

Conclusions

In this paper, the problem of the taxonomic affiliation of the small Eomyid from Sandelzhausen to the species *K. thaleri* is discussed and finally accepted and supported in the light of different arguments. I completely agree with the chronology proposed by Heissig (1997): Sandelzhausen belongs to the Mammalian Neogene unit MN5. Within this unit only one *Keramidomys* species is known upon the whole Europe: *K. thaleri*. This species is older than *K. carpathicus*, which is probably its MN6 descendant.

The teeth measurements on large samples show differences between these two species (M1–2 wider and shorter, m1–2 clearly wider); these two forms were among the smallest known mammals. Their weight did not exceed 5 g, so the measurement errors in the minuscule teeth become more important and these characters are imprecise in a restricted sample.

Finally, in the case of a sufficiently numerous population, despite a certain variability, the morphology seems to be useful for discriminating between these two forms. In *K. thaleri*, the M3s have five lophs and the m3s bear five lophids. In *K. carpathicus* the same teeth have only four. In *K. thaleri* the buccal syncline 1 is larger than in *K. carpathicus*, as are the mesoloph and the mesolophids. Some characters occur only in a few teeth: a complete longitudinal crest can be observed in 10% of *K. thaleri* and likewise a small anteroloph remains in some P4s.

In conclusion, the numerous teeth from Sandelzhausen measured, analysed and compared with other sites suggest that they must be determined as *K. thaleri*, the only European eomyid in MN5.

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References

Aguilar, J.-P., M. Calvet, J.Y. Crochet, S. Legendre, J. Michaux, and B. Sigé. 1986. Première occurrence d'un Mégachiroptère Ptéropodidé dans le Miocène moyen d'Europe (gisement de Lo Fournas IIPyrénées orientales France). *Paleovertebrata* 16: 173–184.

Bolliger, T. 1992. Kleinsäuger aus der Miozänmolasse der Ostschweiz. *Documenta Naturae* 75: 1–296.

Daxner-Höck, G. 1998. Säugetiere (Mammalia) aus dem Karpat des Korneuburger Beckens. 3. Rodentia Carnivora. *Beiträge zur Paläontologie* 23: 367–407.

de Bruijn, H., L. Van Den Hœck Ostende, E. Kristkoiz-Boon, M. Rummel, C. Theocharopoulos, and E. Unay. 2003. The rodents lagomorphs and insectivores from the middle Miocene locality Çandir (Anatolia). *Courrier Forschungsinstitut Senckenberg* 240: 51–87.

Engesser, B. 1979. Relationships of some insectivores and rodents from the Miocene of North America and Europe. *Bulletin of the Carnegie Museum of Natural History* 14: 1–68.

Engesser, B. 1990. Die Eomyidae (Rodentia Mammalia) der Molasse der Schweiz und Savoyens. Systematik und Biostratigraphie. *Schweizerische Paläontologische Abhandlungen* 112: 1–144.

Engesser, B. 1999. Family Eomyidae. In *The Miocene land mammals of Europe*, ed. K. Heissig, and G.E. Rössner, 319–335. Munich: F. Pfeil.

Fahlbusch, V. 1975. Die Eomyiden (Rodentia Mammalia) der oberen Süßwasser-Molasse Bayerns. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 15: 63–90.

Fahlbusch, V. 1979. Eomyidae-Geschichte einer Säugetierfamilie. *Paläontologische Zeitschrift* 53: 88–97.

Fahlbusch, V. 2003. Die miozäne Fossil-Lagerstätte Sandelzhausen–Die Ausgrabungen 1994–2001. *Zitteliana* 43: 109–121.

Fahlbusch, V., and T. Bolliger. 1996. Eomyids and Zapodids (Rodentia Mammalia) in the middle and upper Miocene of Central and Southeastern Europe and the Eastern Mediterranean. In *The evolution of Western Eurasian Neogene mammal Faunas*, ed. R. Bernor, V. Fahlbusch, and H.-W. Mittmann, 208–212. New York: Columbia University Press.

Fahlbusch, V., and W. Wu. 1981. Puttenhausen: Eine neue Kleinsäuger-Fauna aus der Oberen Süßwasser-Molasse Niederbayerns. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie München* 21: 115–119.

Fejfar, O. 1974. Die Eomyiden und Cricetiden (Rod. Mam.) des Miozäns der Tschechoslowakei. *Paleontographica* 146: 100–180.

Hartenberger, J.L. 1967. Les rongeurs du Vallésien (Miocène supérieur) de Can Llobateres (Sabadell Espagne): Gliridae et Eomyidae. Bulletin de la Société Géologique de France (1966) 7e série (8): 596–604.

Heissig, K. 1989. Neue Ergebnisse zur Stratigraphie der mittleren Serie der Oberen Süsswassermolasse Bayerns. Geologica Bavarica 239–257.

Heissig, K. 1997. Mammal faunas intermediate between the reference faunas of MN 4 and MN 6 from the Upper freshwater molasse of Bavaria. In Aguilar, J-P., Legendre, S. and Michaux, J. eds., Actes du Congrès Biochrom'97 Biochronologie mammalienne du Cénozoïque en Europe et domaines reliés. Mémoires et Travaux de l'Institut de Montpellier: 537–546.

Höck, V., G. Daxner-Höck, H.P. Schmid, D. Badamgarav, W. Frank, G. Furtmueller, O. Montag, R. Barsbold, Y. Khand, and J. Sodov. 1999. Oligocene–Miocene sediments, fossils and basalts from the Valley of Lakes (Central Mongolia)–an integrated study. *Mitteilungen der Österreichischen Geologischen Gesellschaft Wien* 90: 83–125.

Hugueney, M., and P. Mein. 1968. Les Eomyidés (Mammalia Rodentia) Néogènes de la région lyonnaise. *Geobios* 1: 187–204.

Kälin, D. 1997. The Mammal zonation of the Upper marine molasse of Switzerland reconsidered. A local bio-zonation of MN 2-MN 5. In Aguilar, J-P.; Legendre, S. & Michaux, J. eds., Actes du Congrès Biochrom'97Biochronologie mammalienne du Cénozoïque en Europe et domaines reliés. Mémoires et Travaux de l'Institut de Montpellier: 515–535.

Kowalski, K. 1967. Rodents from the Miocene of Opole. *Acta Zoologica Cracoviensia* 12: 1–18.

Kowalski, K., and B. Rzebik-Kowalski. 2002. Paleoecology of the Miocene fossil mammal fauna from Belchatow (Poland). *Acta Theriologica* 47(suppl.1): 115–126.

Mörs, T., F. van der Hocht, and B. Wutzler. 2000. Die erste Wirbeltierfauna aus der miozänen Braunkohle der Niederheinischen Bucht (Ville-Schichten Tagebau Hambach). *Paläontologische Zeitschrift* 74(1/2): 145–170.

Moser, M., Rössner, G.E., Göhlich, U.B., Böhme, M., and Fahlbusch, V. 2009. The fossil lagerstätte Sandelzhausen (Miocene; southern Germany): history of investigation, geology, fauna and age. In: Rössner, G.E. & Göhlich, U.B.: Fossil lagerstätte Sandelzhausen (Miocene, southern Germany): Contributions to the fauna. Paläontologische Zeitschrift 83 (1): 000–000.

Qiu, Z.-D., and X.-M. Wang. 1999. Small mammal Faunas and their ages in Miocene of Centra Nei Mongol (Inner Mongolia). *Vertebrata Palasiatica* 37: 134–138.

Sach, V.J. 1999. Litho-,und biostratigraphische Untersuchungen in der Oberen Süßwassermolasse des Landkreises Biberach a. d. Riss (Oberschwaben). Stuttgarter Beiträge zur Naturkunde Ser. B: 1–167.

Schaub, S., and H. Zapfe. 1953. Die Fauna der miozänen Spaltenfüllung von Neudorf an der March (CSR) Simplicidentata. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschafliche Klasse* 162: 181–215.

Schlosser, M. 1926. Die Säugetierfaune von Peublanc (Dép. Allier). *Societé des Sciences Naturelles de Croatie (Kramberger Festband)* 38(39): 372–393.

Schötz, M. 1979. Neue Funde von Eomyiden aus dem Jungtertiär Niederbayerns. *Aufschluss* 30: 465–473.

Shotwell, J.A. 1956. Hemiphillian mammalian assemblage from Northeastern Oregon. *Bulletin of the Geological Society of America* 67: 717–738.

Stehlin, H.G., and S. Schaub. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweizerische Paläontologische Abhandlungen* 67: 1–385.

Unay, E., and H. de Bruijn. 1984. On some Neogene rodent assemblages from both sides of the Dardanelles Turkey. *Newsletters on Stratigraphy Berlin* 13(3): 119–132.

Ziegler, R. 1995 . Die untermiozänen Kleinsäugerfaunen aus den Süßwasserkalken von Engelwies und Schellenfeld bei Sigmaringen (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde B: 1–53.